THE ALIMENTARY CANAL OF PASSALUS*

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INTRODUCTION

It has long been known that the alimentary canal of *Passalus cornutus* Fab. harbors an extensive associated flora and fauna. Also, its sub-social habits have attracted some attention. Because of this and its specialized food habits *Passalus* offers an interesting problem in tracing the results of such specialization upon the digestive canal. This paper is not intended as a final and complete work, but more as a preliminary discussion dealing especially with the morphology of the alimentary tract.

The writer wishes to express his appreciation to Mr. A. A. Mathewson, who did half of the work in the preparation of the slides and then accepted a position precluding further study, and to Dr. C. H. Kennedy, under whose direct supervision this work has been carried on.

Leidy (1851) first called attention to the flora and fauna in the hind intestine of *Passalus cornutus*. He gives a short description of the alimentary tract using a slightly different terminology from that generally used at present. Considering the attachment of the Malpighian tubules as a landmark in setting off the hind-intestine from the mid-intestine, the proventriculus as used by Leidy consists of the fore-intestine and the mid-intestine, which includes the ventriculus or true-stomach. The ventriculus as used by Leidy is a part of the hind-intestine, since it is set off from the mid-intestine by the attachment of the Malpighian tubules and is lined with a chitinous intima. This part of the hind intestine is here considered as the ileum and harbors the extensive flora and fauna as described by Leidy. The flora of fungi is limited to the distal portion of the ileum, which is characterized by numerous sacculi or folds of the intestinal wall.

In all the beetles examined, these fungus gardens were present and it seems that their occurrence is regular in the specialized ileum of *Passalus cornutus*. Mr. R. H. Painter, of this department, has successfully cultured two of these fungi.

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Leidy describes several fungi, *Enterobryus attènuatus*, *Arthromitus cristatus*, *Cladophytum comatum*, and *Corynocladus radiatus*, as being fixed parasitic on the mucous membrane of the intestine. He also describes an elongated tubular cellule and a granulo-filamentous phytoid substance as parasitic phytoid bodies, the exact nature of which he was uncertain, and several pseudo-entophyta. *Gregarina Passalicornuti* and *Hystrignathus rigidus* are listed as being associated with the flora of the intestinal canal.

The relation of many insects to micro-organisms has occupied the attention of a few investigators. It has been shown in some cases, Baumberger (1919), that micro-organisms furnish food for the insects. In others the organisms exist as parasites, while in some a symbiotic relationship occurs, as Cleveland (1924) has proved to be the case with termites. Leidy considers these organisms as being parasitic within the alimentary tract of *Passalus*. However, their regular occurrence and the specialized food habits of the beetle suggests the possibility that this may not necessarily be so. Some of these intestinal fungi may play an important part in the physiology of digestion. Further work on the digestion and the embryology of the alimentary tract seems to be necessary to clear up this relationship. Leidy pointed out that the millipede, *Julus marginatus*, which also lives on decaying and rotting wood, has an extensive floral and faunal association.

The Gross Anatomy of the Adult Canal.

The alimentary canal of the adult beetle shows considerable specialization in form and structure. In accordance with the general rule that in herbiverous insects the alimentary tract is longer than in carniverous insects, in *Passalus* it is a winding convoluted tube about three times as long as the body. The canal makes three complete loops and turns back on itself twice. Three chief divisions of the tract are readily recognized, which are the fore-intestine (stomodeum), the mid-intestine (mesenteron or ventriculus), and the hind intestine (proctodeum). The general form of the gross anatomy is shown in Fig. 1.

The fore-intestine is a straight, comparatively short tube extending from the mouth to about the beginning of the meso thorax. The pharynx is evident as a slight dilation of the trac in the head. The oesophagus is a slender elongate tube, extend-

ing into the prothorax, where it gradually enlarges to form the crop. The mid-intestine is separated from the fore-intestine by a constriction composed of two distinct rings.

The mid-intestine is a long coiled tube making three complete loops. It is almost uniform throughout and excepting the posterior tip is covered by numerous small papillae, which are crypts or diverticula of the digestive epithelium. These give it a white maculated appearance.

The hind-intestine, which is somewhat shorter in length than the mid-intestine, is divided into four regions. Poyarkoff (1910) recognized four parts in the hind intestine of a Chrysomelid, *Gallerucella luteola*, according to Wood (1916). There are four distinct divisions of the hind intestine of *Passalus* which are considered as the proximal portion of the ileum, the distal portion of the ileum, the colon, and the rectum. The first region, the proximal portion of the ileum, is comparatively short and appears much the same as the mid-intestine, except that it is not covered by papillæ. The distal portion of the ileum is much larger and longer and is characterized by numerous large folds of the intestinal wall. It is in these folds that the intestinal fungi live. This part of the ileum extends almost directly caudad for over half of its length and then turns cephalad. The colon is a long, slender tube forming a large semicircle on top of the coiled ventriculus, straightening out towards the tip of the abdomen. The rectum is short, but is evident as a slight enlargement of the tract somewhat lighter in color than the colon.

For a discussion of the mouthparts and skeletal elements, see Landacre (1902).

The succeeding discussion of the histological structure of the alimentary canal is taken up in order, beginning at the anterior end.

The Histological Structure of the Fore-Intestine.

Pharynx.—In *Passalus* this region is evident as a slight enlargement of the tract with a heavy chitinous lining continuous with that of the body wall. The primary intima is covered with fine chitinous spines which project caudad. The secondary intima appears slightly fibrillar, almost transparent, and is much thicker than the primary intima. The epithelium consists of a definite layer of small irregular cells. The muscle layers are much the same as in the oesophagus.

Oesophagus.—The intima of the oesophagus is thrown into a series of longitudinal folds (Fig. 2). These are irregular and usually are six in number. The primary intima is well developed and is covered by numerous spines of varying lengths. The secondary intima is much thicker and is almost transparent. (Fig. 3).

The epithelium of the oesophagus consists of irregular cuboidal cells. The basement membrane is present.

The longitudinal muscles form a layer covering the epithelium. They do not all run directly longitudinally, but intertwine considerably, so that cross-sections of this region show many of them running in an oblique fashion. All sections made show that the space between the epithelium and circular muscular layer is not completely filled by these longitudinal muscles.

The circular muscles form a layer covering the longitudinal muscles. This layer varies somewhat in thickness and forms a complete covering around the tract.

Crop.—In the crop the lumen is wider than in the oesophagus, the epithelium is thinner, and the chitinous folds are much smaller.

The primary intima is thin and lacks the chitinous teeth of the oesophagus. The secondary intima is much thicker and is almost transparent.

The epithelial cells of the crop are much like those of the oesophagus, except that in places instead of being cuboidal they are flattened. In some of them appear irregular sphere-like bodies, somewhat larger than the nuclei and which stain black with Delafield's haemotoxylin and eosin. The identity and nature of these Rickettsia-like bodies is undetermined. They are found only in the crop and in that portion of the fore-intestine forming the fold of the oesophageal valve. The basement membrane is well defined.

The longitudinal muscles are much less in evidence than in the oesophagus. Anteriorly they continue into the oesophagus and posteriorly end in the fold of the oesophageal valve. (Fig. 11).

The circular muscles are more in evidence than the longitudinal muscles. They form a complete layer around the canal much the same as in the oesophagus.

Oesophageal Valve.—In the transition from the fore-intestine to the mid-intestine, the fold of tissue composing the oesophageal

valve is well developed (Fig. 11). The structure of the wall of the fold is much like that of the wall of the crop. Intima, epithelium, basement membrane, longitudinal and circular muscle layers are present. The intima ends gradually, in longitudinal section, coming to a point on the posterior face of the valve.

The intima disappears on the posterior face of the fold which marks the limits of the fore-intestine.

The epithelial cells of the anterior face of the oesophageal valve continue much the same as in the crop until just before reaching the tip of the fold. Here the cells begin to elongate and become gradually longer on the posterior face of the valve until the end of the fore-intestine is reached. At this point a ring of spindle-shaped cells is encountered, which terminates the epithelium of the fore-intestine. The turgid appearing digestive epithelial cells follow immediately after this ring of spindle-shaped cells.

The exact nature of this ring of spindle-shaped cells is undetermined. It marks the limits of the fore-intestine and possibly may be the imaginal disc of some authors. The nuclei of these spindle-shaped cells contain almost no deep-staining chromatin material, whereas, the nuclei of both the epithelial digestive cells of the stomach and the epithelial cells of the fore-intestine contain much deep staining material. The basement membrane is continuous from the fore-intestine to the mid-intestine.

The longitudinal muscles of the fore-intestine end near the tip of the anterior face of the oesophageal valve. In the tip of the fold there are no muscles whatever. On the posterior face of the fold the longitudinal muscles of the mid-intestine begin. They are fewer in number and smaller than those of the fore-intestine.

The circular muscles of the fore-intestine end at about the middle of the anterior face of the oesophageal valve. At this point they are much smaller in size than the longitudinal muscles. The circular muscles of the mid-intestine appear soon after the longitudinal muscles of the mid-intestine begin. They are small isolated strands.

The peritoneal membrane is not concerned in the fold of the valve, but is continuous from the fore-intestine to the mid-intestine. Along with it run several fibers of longitudinal muscle.

THE MID-INTESTINE.

The mid-intestine or ventriculus is an elongate tube, a little longer than the body of the insect itself, and is almost uniform throughout, (Fig. 1). It is characterized principally by the numerous crypts or diverticula of the stomach wall, by the absence of a chitinous intima, and by the presence of large secretive epithelial cells, (Fig. 4).

Peritropic Membrane.—In the ventriculus of *Passalus* the secretion of digestive fluids by the epithelial cells forms a granular layer. Its inner border usually forms, as shown by cross-sections, a distinct dark staining line known as the peritropic membrane. In places it can be seen that the entire mass separates from the epithelial cells. The usual explanation given is that this process continues indefinitely and the peritropic membrane shrinks around the food in the lumen of the gut, while new membranes are repeatedly being formed by the discharging epithelial cells. The peritropic membrane extends from the oesophageal valve at the anterior end of the ventriculus into the hind-intestine to about the middle of the proximal portion of the ileum.

The epithelium of the ventriculus forms the layer of cells whose function it is to secrete the digestive fluids into the lumen of the gut. In *Passalus* we find a very specialized condition for, apparently, secretion is both holocrine and merocrine. It is holocrine in the epithelium of the central canal and merocrine in the epithelial cells at the bottom of the crypts.

Commonly the wall of the ventriculus of beetles is evaginated to form crypts or diverticula which increase the digestive surface. This holds true in *Passalus* and a single cross-section near the center of the ventriculus shows about sixty of these crypts, (Fig. 4). At the bottom of each crypt are broad epithelial cells, each connected to a common opening by a short canal. Each canal is lined by a dense layer of dark staining substance which is known as the *striated border.* As pointed out above, the type of secretion from these epithelial cells is merocrine.

In the neck of each crypt the epithelial cells are of a different nature, being elongate and turgid appearing. This type of cell completely lines the central canal of the ventriculus. Secretion is holocrine, that is, the entire cell contents are discharged into the lumen of the gut, and the discharged cells are replaced from embryonic nests of "nidi."

From a few of the crypts in the wall of the ventriculus are gland-like appearing evaginations. They are densely filled with dark staining nuclei. The nature and function of these nuclear crypts is undetermined, (Fig. 5). The basement membrane of the ventriculus is present.

The circular muscles form two distinct layers. The first is very thin and is composed of fibers circling the central tract of the ventriculus, but they do not extend over the crypts. They frequently run obliquely and cross each other in an irregular manner. The second layer of circular muscles forms a thin incomplete layer on top of the crypts in a twisted fashion.

The longitudinal muscles of the ventriculus are small and isolated among the fibers of the second layer of circular muscles.

The wall of the crypts apparently contains no muscular layers, but is covered by a peritoneal membrane of connective tissue.

The Transition from the Mid-Intestine to the Hind-Intestine.

The hind-intestine is set aside from the mid-intestine by a fold of tissue called the pyloric valve. In *Passalus* this is not a true valve in the sense that it closes the tract at this point, but it is a fold of tissue marking the transition from the mid-intestine to the hind-intestine. The size of this fold is so small in comparison to the width of the tract at this point that it could have little significance as a valve in closing the tract. However, since there are two distinct folds, one immediately following the other, it is here considered as the pyloric valve.

The Pyloric Valve.—Sections from several different beetles showed the form of the folds to vary considerably, but the anterior fold is always much smaller than the posterior one. The intima first appears at the beginning of the anterior fold and is smooth over the entire valve. The epithelial cells are elongate and regular. Fibers of longitudinal muscles extend into the folds, (Fig. 7).

The peritropic membrane is continuous from the mid-intestine into the proximal portion of the ileum.

The intima of the hind-intestine appears on the anterior fold of the valve and both primary and secondary intima are clearly evident. The primary intima is smooth over the folds of the valve, but in the ileum is covered by posteriorly projecting spines.

The epithelium is continuous from the mid-intestine to the hind-intestine. The digestive epithelial cells cease abruptly at the point of the beginning of the first fold of the valve and the point where the intima of the hind-intestine begins. In the valve the cells appear elongate and regular, whereas in the ileum they are cuboidal and irregular. The basement membrane is continuous from the mid-intestine to the hind-intestine.

The circular muscles appear as being continuous from the mid-intestine to the hind-intestine. With the beginning of the valve there appears an additional set of circular muscles lying between the epithelium and the longitudinal muscles. Thus in this region there appears three layers of muscles which are: a layer of inner large circular muscles, a layer of longitudinal muscles and a layer of outer smaller circular muscles occurring as isolated strands in the longitudinal layer.

The longitudinal muscles appear as a thin continuous layer from the mid-intestine to the hind-intestine. Fibers extend into the folds of the valve.

The Hind-Intestine

The first division of the hind-intestine may be divided morphologically into two parts, the proximal and distal portions of the ileum. The proximal portion extends from the beginning of the hind intestine to the beginning of the intestinal coecom. The distal region composes the remainder of the ileum and is characterized by large folds in the wall which harbor the intestinal fungi, (Fig. 1).

The Proximal Portion of the Ileum.—The primary intima is evident from the beginning of the folds of the pyloric valve. It is smooth over the valve and then gradually becomes roughened so that posteriorly projecting teeth are developed. The secondary intima is much thicker than the primary intima, is almost transparent, and shows little difference in the two divisions of the ileum.

The epithelial cells are cuboidal and irregular. The basement membrane is clearly evident.

The circular muscles of the proximal portion of the ileum are largely confined to a layer between the epithelium and the incomplete layer of longitudinal muscles. The layer becomes gradually thicker towards the distal portion of the ileum. The muscles are much larger than those of the mid-intestine, (Fig. 7).

The longitudinal muscles are evident as a thin incomplete layer on top of the circular muscles. These disappear entirely at about the point of the beginning of the intestinal coecum.

The Distal Portion of the Ileum.—The wall of this part of the ileum is folded to form six series of about twenty chambers, (Fig. 10). It is in these chambers that the intestinal fungi are found, though a few are wound around the spines found throughout this region of the ileum. The particles of chewed up wood are mainly confined to the central canal and are not found in the bottoms of the chambers.

The intima is covered by numerous long sharp spines, except in the bottoms of the chambers. Here the intima is merely roughened. The secondary intima is much the same throughout and appears slightly granular and almost transparent, (Fig. 12).

The epithelial cells are irregular, cuboidal, and about the same thickness as the secondary intima. A basement membrane is present.

A layer of circular muscles covers the epithelial cells and forms a complete layer several strands in thickness.

Longitudinal muscles are absent in the distal portion of the ileum.

The intestinal coecum is an enlargement of one of the intestinal folds characteristic of the distal portion of the ileum, (Fig. 1). In histological structure it is the same as that of the distal portion of the ileum.

Transition from Ileum to Colon.

In the region of the transition from the ileum to the colon there is a fold in the wall of the tract which is considered as the intestinal valve, (Fig. 8). In all of the beetles sectioned, the fold was always retracted and whether it can be extended to close the tract at this point was not determined.

The intima in the fold is smooth and lacks the chitinous spines which cover the intima of the main tract. Otherwise there is no difference in the intima, epithelium, and basement membrane which are concerned in the fold. The spines gradually become shorter and disappear entirely a short distance past the valve. Over the fold there are no circular muscles which are characteristic of this region, but instead there is a heavy layer of longitudinal muscles.

The epithelial cells are much the same as in the ileum, except that they gradually become larger and at the point where the circular muscles disappear become more regular and elongate.

The layer of circular muscles becomes smaller and disappears entirely a short distance past the intestinal valve. The epithelium at this point is covered only by a peritoneal membrane.

Colon.—The intima in the colon is smooth and somewhat thinner than in the ileum. The primary intima is a thin dark staining layer, while the secondary intima is a thicker and almost transparent layer, (Fig. 6).

The epithelial cells are comparatively regular and elongate. Through most of the colon the wall of the tract is largely epithelium. Towards the distal end the cells become larger, more elongate, and more regular. Nuclei show clearly throughout. At the distal end the wall of the tract is thrown up into six divisions corresponding to the six divisions of the muscles of the colon, (Fig. 9). A basement membrane is present.

Circular muscles are not present in the colon.

Longitudinal muscles are not present at the beginning of the colon, but appear later. They gradually become larger and larger, forming an almost complete covering around the tract. They disappear entirely at the end of the colon.

Rectum.—The intima of the rectum is thrown into six folds which at one point almost close the lumen of the gut. The intima is distinct and slightly roughened, but not covered by spines, (Fig. 13).

The epithelial cells are irregular and cuboidal and pile up on each other in the folds. The nuclei are clear and distinct. The cells are several times smaller than the epithelial cells of the colon.

The circular muscles of the rectum appear as a distinct thick layer. The change from the colon to the rectum is very abrupt. The longitudinal muscles disappear and there arises immediately a heavy layer of circular muscles, (Fig. 14). In a short distance the musculature reaches its greatest development and gradually tapers off to the anus. The muscles are divided into six regions by six radial connective tissue (?) septa, (Fig. 13).

Longitudinal muscles are absent in the rectum.

MALPIGHIAN TUBULES.

In the adult beetle there are four Malpighian tubules which are long and thread-like. Each is attached to the alimentary canal at a single place which is at the point of transition from the mid- to the hind-intestine. The two dorsal tubes are evident in a dorsal dissection passing caudad and disappearing under a fold of the stomach. The two ventral tubes pass under the same fold of the stomach and the four tubes come in contact with the colon at about half way from the ileum to the rectum. They appear on the colon as a maze of convoluted tubes and eventually two of them extend along the posterior portion of the colon where they end blindly in the body cavity attached to tracheae. The other two tubes extend forward and cross to the stomach, forming a mass of convoluted tubes. They extend along the anterior portion of the stomach, where they end blindly in the body cavity.

Histologically the layers of the wall in the Malpighian tubules are the same as in the rest of the hind-intestine. The intima is very thin and irregular. The epithelium consists of irregular cuboidal cells which constitute the greater part of the wall. A basement membrane is present and the muscular layers are absent.

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EXPLANATION OF PLATES.

PLATE I.

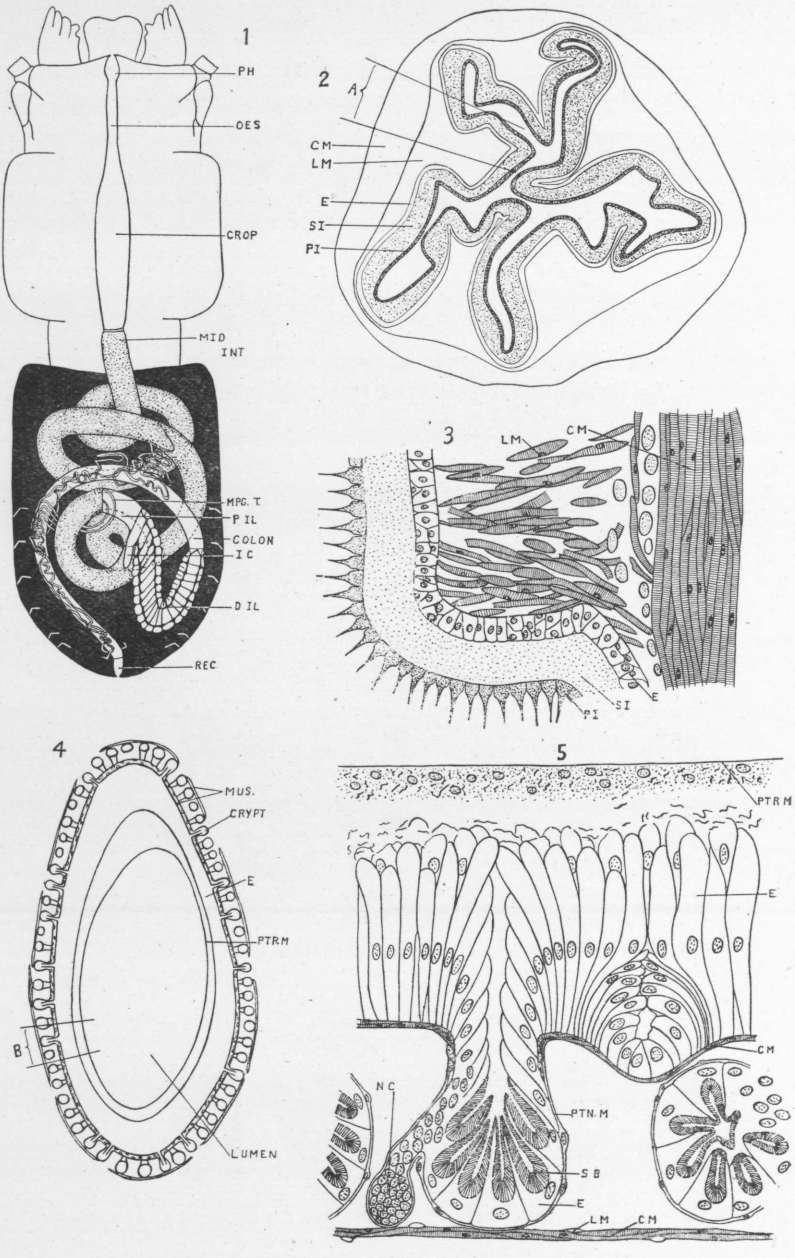
Fig. 1. Dorsal view of adult *Passalus* showing alimentary canal.
Fig. 2. Cross-section of Oesophagus.
Fig. 3. Section "A" of Fig. 2 enlarged.
Fig. 4. Cross-section through central part of mid-intestine.
Fig. 5. Section "B" of Fig. 4 enlarged.

PLATE II.

Fig. 6. Section "C" of Fig. 9 enlarged.
Fig. 7. Longitudinal section through pyloric valve.
Fig. 8. Longitudinal section through intestinal valve.
Fig. 9. Cross-section of colon near posterior end.
Fig. 10. Cross-section of distal portion of ileum.
Fig. 11. Longitudinal section of oesophageal valve.
Fig. 12. Section "D" of Fig. 10 enlarged.
Fig. 13. Cross-section of rectum.
Fig. 14. Section "E" of Fig. 13 enlarged.

ABBREVIATIONS USED IN THE FIGURES.

PH—Pharynx
OES—Oesophagus
MID INT—Mid-intestine
MPG T—Malpighian tubules
P IL—Proximal ileum
I C—Intestinal coecum
D IL—Distal ileum
REC—Rectum
C M—Circular muscle
L M—Longitudinal muscle
E—Epithelium
S I—Secondary intima
P I—Primary intima
MUS—Muscle
PTR M—Peritropic membrane
PTN M—Peritoneal membrane
S B—Striated border
N C—Nuclear crypt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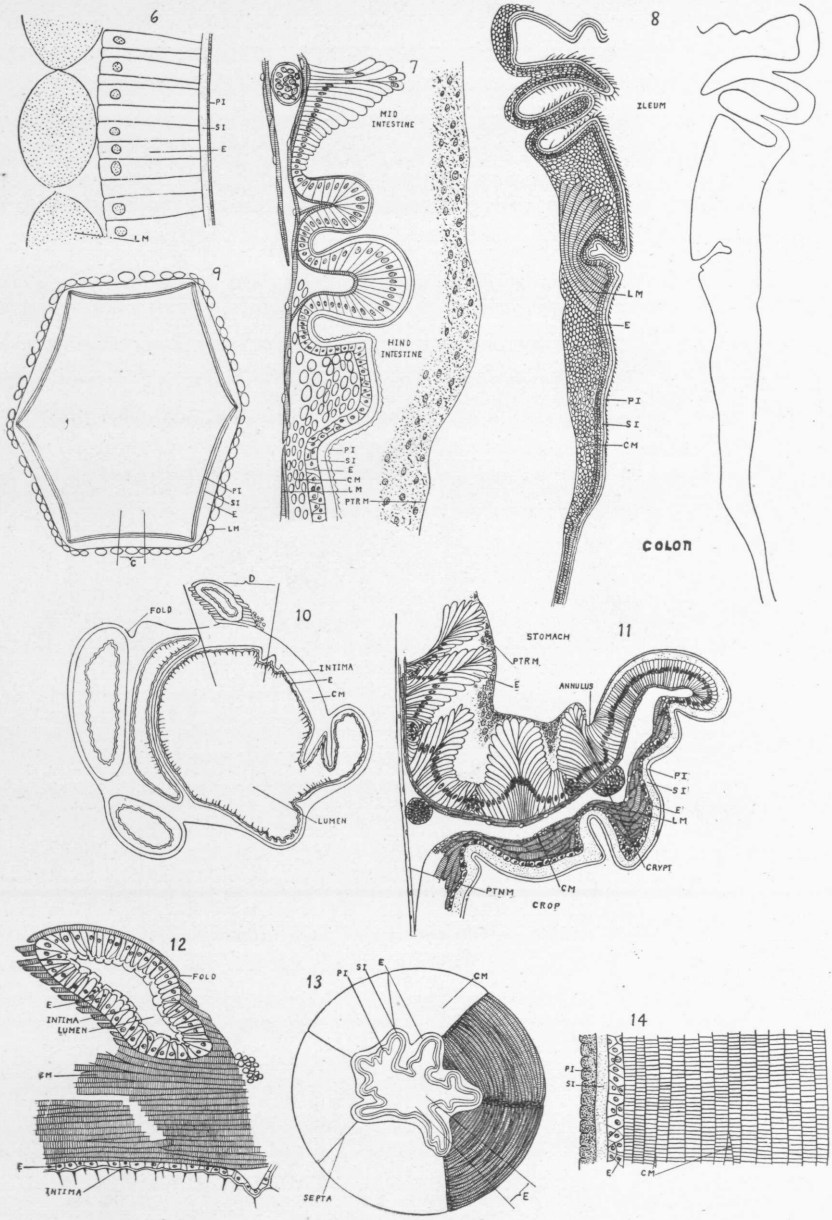
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